

Surface water and ground-water thresholds for maintaining *Populus–Salix* forests, San Pedro River, Arizona

S.J. Lite ^{*}, J.C. Stromberg

School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

Received 2 February 2004

Available online 26 May 2005

Abstract

Ground-water and surface flow depletions are altering riparian ecosystems throughout the southwestern United States, and have contributed to the decline of forests of the pioneer trees *Populus fremontii* (Fremont cottonwood) and *Salix gooddingii* (Goodding willow). On some rivers, these forests have been replaced by shrublands of *Tamarix ramosissima* (tamarisk), a drought-tolerant species from Eurasia. The physiological response of these three riparian plant species to decreases in water availability is well studied, but little attention has been given to shifts in community and population structure in response to declines in surface flow and ground-water levels. Based on study of 17 sites spanning a hydrologic gradient, this research identified hydrologic thresholds above which *P. fremontii–S. gooddingii* maintain tall dense stands with diverse age classes, and above which they are more abundant than *T. ramosissima* stands along the San Pedro River in Arizona. Surface flow permanence was the hydrologic variable that explained most of the variance in species abundance and relative importance, with inter-annual ground-water fluctuation and depth to ground water also contributing. *P. fremontii* and *S. gooddingii* were dominant over *T. ramosissima* at sites where surface flow was present more than 76% of the time, inter-annual ground-water fluctuation was less than 0.5 m, and average maximum depth to ground water was less than 2.6 m, during a two-year period of data collection. Because *T. ramosissima* is a shrub species with smaller leaves and lower canopy heights than *P. fremontii* and *S. gooddingii*, these shifts in species composition corresponded to decreases in maximum canopy height and upper stratum (above 8 m) vegetation volume as site water availability declined. As well, sites with deeper water tables and more intermittent flows had greater areal coverage of shrublands and less of woodlands. The altered vegetation structure along dewatered rivers may lower wildlife habitat quality. This study provides river managers with quantitative hydrologic guidelines for conserving tall dense *P. fremontii–S. gooddingii* stands and emphasizes the importance of maintaining long-term hydrologic conditions that are favorable to these species. The study also has implications for riparian restoration and invasive species management by suggesting that desired outcomes may be achieved through restoration of physical processes.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: *Populus*; *Salix*; *Tamarix*; Invasive species; Ground-water thresholds; Restoration

1. Introduction

Many riparian tree species are phreatophytic, meaning they extract water from aquifers or the capillary fringe above the water table. The phreatophytes that grow along rivers in the southwestern United States

encompass a diverse group of species that differ widely in root depth and architecture, water use rate, tolerance to drought and declining and fluctuating water tables, and capacity to shift between seasonally varying water sources. Some, such as *Salix gooddingii* (Goodding willow), appear to be obligate phreatophytes that require permanently available shallow ground water (defined here as the zone of saturation) (Busch et al., 1992; Horton et al., 2001a,b). *Populus fremontii* (Fremont cottonwood) trees also are phreatophytic,

^{*} Corresponding author.

E-mail address: sjoylite@earthlink.net (S.J. Lite).

although they may be able to tolerate deeper and more fluctuating water tables than *S. gooddingii* and use a greater quantity of soil moisture from precipitation and unsaturated soils than *S. gooddingii* (Snyder and Williams, 2000). *Tamarix ramosissima* (tamarisk) is a deep-rooted, facultative phreatophyte that obtains water from saturated and unsaturated soil and is physiologically adapted to a higher degree of water stress than are *P. fremontii* and *S. gooddingii* (Busch et al., 1992; Busch and Smith, 1995; Horton et al., 2001a,b). Although primarily phreatophytic in natural river settings, stream base flows can be a water source for *Populus*, *Salix* and other riparian trees growing at the stream edge (Smith et al., 1991). However, the stream base flows themselves may derive from inflowing ground water. Typically, perennial rivers tend to be gaining reaches and have high and stable water tables, whereas reaches of intermittent rivers tend to lose water and have greater and more seasonally variable depths to ground water.

Stream diversion and ground-water pumping for urban, agricultural, and industrial uses have converted many perennial rivers in the southwestern United States to intermittent or ephemeral rivers, and led to declines in ground water across the flood plain and increased inter-annual fluctuation in ground-water depth. This has contributed to the decline of many riparian phreatophytes. Although *P. fremontii*–*S. gooddingii* woodlands have increased on some rivers, hydrologic alterations and agricultural/urban conversion have decreased their distribution on many others, and remain as threats to this ecosystem type (NatureServe, 2003). Consequences of declines in riparian forests include loss of habitat for animal species and loss of scenic areas for recreation. Riparian vegetation loss also can contribute to increased flood peaks, erosion, and channel widening. Many people value these forests and their functions, and thus there is considerable interest in restoring *Populus*–*Salix* forests along degraded river reaches and conserving those forests that remain. These restoration and management activities require knowledge of species relationships with abiotic factors and processes including hydrologic regimes. Conservationists and managers also benefit from knowing hydrologic threshold values for desired attributes such as community structural traits and species abundances.

“Thresholds of probable concern” have been defined as “upper and lower levels of change in selected biotic and abiotic variables which act as indicators of the acceptability of ecosystem condition” (Rogers and Biggs, 1999). Precisely determining the physical thresholds that maintain desired biotic conditions can be difficult. With respect to ground-water depths to maintain particular tree species, for example, thresholds may vary among rivers because of variations in climate, historic hydrologic setting, and ecotypic species variation (Shafroth et al., 2000; Lesica and Miles, 2001; Sexton et al.,

2002). The thresholds also vary depending on management goals, i.e., what ecosystem condition is considered acceptable. Acceptable ecosystem condition may be the presence of a desired species or association, the dominance of that species or association in the ecosystem, or a forest structure sufficient to supply particular ecological functions. Abiotic thresholds vary accordingly. For example, *P. fremontii* trees may grow along dry riverbeds where water tables are only seasonally high or where mean depths exceed 5 m (Stromberg et al., 1996). However, forests in such situations tend to be sparse and of low age class diversity, and thus may not provide the desired benefits. *P. fremontii* and *S. gooddingii* are drought-sensitive species (Leffler et al., 2000) and dense, multi-aged forests of the *P. fremontii*–*S. gooddingii* association appear to be restricted to perennial or intermittent rivers where depth to ground water remains less than 4 m. These values are derived from descriptive studies of plant distribution and physiological monitoring of trees across spatial or temporal ground-water gradients along rivers in the deserts (Mojave, Sonoran, Chihuahuan) of the US Southwest (Stromberg et al., 1991, 1996; Shafroth et al., 1998, 2000; Horton et al., 2001a,b).

In addition to causing declines of *P. fremontii* and *S. gooddingii*, hydrologic changes to rivers have influenced the abundance of drought-tolerant species such as *T. ramosissima*. *Tamarix* species were introduced to the United States in the early 1800s (Horton, 1964) from Europe and Asia for ornamental, windbreak, and erosion control purposes. They have since spread to water courses throughout the United States and now cover large acreage in many western states (Zavaleta, 2000), including large expanses of former *P. fremontii*–*S. gooddingii* forest on large, low-elevation desert rivers. Stream diversion, ground-water pumping, and flood flow alteration below dams have contributed to this shift in species composition, allowing *T. ramosissima* (and closely related species) to attain dominance in reaches with hydrologic conditions that are no longer favorable to *P. fremontii* and *S. gooddingii* (Shafroth et al., 1998, 2002; Stromberg, 1998; Levine and Stromberg, 2001; Stromberg and Chew, 2002; Tallent-Halsell and Walker, 2002).

The mechanism of the *Populus*–*Salix* to *Tamarix* shift is either passive replacement due to abiotic constraints or active displacement through competitive pressure by *Tamarix*. The degree to which *T. ramosissima* may be contributing to decline of *P. fremontii*–*S. gooddingii* forests by reducing water availability is a topic under debate (Stromberg and Chew, 2002). Some have speculated that *T. ramosissima* uses larger quantities of water than other riparian trees and thus may desiccate alluvial aquifers, making conditions unfavorable to *P. fremontii* and *S. gooddingii* (Smith et al., 1998; Cleverly et al., 1997). However, studies that measure evapotranspiration rates have varied in temporal and spatial scales, and

environmental context, making it difficult to draw conclusions on relative water use rates of the different riparian species (Busch et al., 1992; Sala et al., 1996; Cleverly et al., 2002). While removal experiments show that *Tamarix* trees can have negative effects on *Salix* neighbors (Busch and Smith, 1995), other studies indicate that *Tamarix* does poorly under *Populus* canopy (Lesica and Miles, 2001). As well, field and pot studies have shown that as a seedling, *Tamarix* is not a strong competitor against co-establishing *Populus* and *Salix*, suggesting that active displacement by *Tamarix* is an unlikely mechanism for its dominance (Sher et al., 2000, 2002; Sher and Marshall, 2003).

Questions over whether the mechanism is passive replacement or active displacement also has spurred debate over ways to restore riparian ecosystems. Methods such as burning, herbicide, mechanical removal, or biologic control of *Tamarix* spp. are frequently employed, often with the hope that once *Tamarix* spp. is removed, *Populus* spp. and *Salix* spp. will establish (Taylor and McDaniel, 1998; Quimby et al., 2003). This may occur if physical conditions that are favorable to *Populus* spp. and *Salix* spp., such as shallow ground-water tables and appropriately timed floods, are restored. However, if conditions remain unfavorable for these replacement species, *Tamarix* spp. may persist or other species with similar traits may establish. Restoring hydrologic conditions that are favorable to *P. fremontii* and *S. gooddingii* may not only allow *P. fremontii* and *S. gooddingii* to establish, but also decrease *T. ramosissima* cover (Lesica and Miles, 2001; Sher et al., 2000, 2002; Sher and Marshall, 2003). There is a need to refine the thresholds at which this shift in composition occurs and to determine levels and temporal patterns of ground-water depth at which drought-tolerant species dominate.

We conducted this study to: (1) identify hydrologic thresholds for maintaining *P. fremontii*–*S. gooddingii* forests; (2) quantify changes in *P. fremontii*, *S. gooddingii*, and *T. ramosissima* population stand structure traits (size class diversity, canopy cover, basal area, vegetation volume, and stem density) across gradients of ground-water depth and fluctuation and surface flow permanence; and (3) assess how community composition and biomass structure vary across these hydrologic gradients. We hypothesized that ground-water depth and inter-annual ground-water fluctuation would be prime determinants of the relative abundance of *P. fremontii* and *S. gooddingii* vs. *T. ramosissima*, with surface flow permanence playing a lesser role. Although the results are specific to the San Pedro River, our goal was to generate models that can be tested on other regional rivers. Ultimately, we wish to provide information that will assist river managers in conserving and restoring high density *P. fremontii*–*S. gooddingii* forests.

2. Methods

2.1. Study area

We measured abundance and structural traits of *P. fremontii*–*S. gooddingii*–*T. ramosissima* forests across spatial gradients of ground-water and surface water availability, along the San Pedro River in southeastern Arizona, USA. We refer to this species as *T. ramosissima* but note that species determination in the *Tamarix* genus can be difficult; *T. ramosissima* and *Tamarix chinensis* are morphologically very similar, and although disjunct in Asia, freely hybridize where they have been brought into proximity in North America (Gaskin and Schaal, 2002). A hybrid of these two species may be the common form on many western rivers, including the San Pedro.

The San Pedro arises in Sonora, Mexico and flows northward through the Chihuahuan and Sonoran Deserts (Fig. 1). Based on geomorphic differences, hydrologists and geomorphologists recognize two sub basins within the San Pedro River Basin (Tuan, 1962). The Upper Basin extends from the headwaters (elevation 1500 m) to a geologic constriction known as the Narrows (elevation 1000 m), and the Lower Basin extends from the Narrows to the confluence with the Gila River (elevation 580 m). Based on data obtained from the Western Regional Climate Center, mean annual (1971–2000) precipitation and temperature are 360 mm and 17 °C in the Upper Basin (Sierra Vista climate station #027880, elevation 1402 m) and 250 mm and 21 °C in the Lower Basin (Florence climate station #023027, elevation 460 m). There are two seasons of high precipitation: summer monsoon (July through September) and winter pacific frontal storms (December and January). The summer monsoon rains are typically fast moving storms accompanied by high winds with large amounts of precipitation occurring over a short time period. The winter rain storms are typically less intense and of longer duration. The stream alluvium of this river is recharged by flood flows from rainstorms throughout the watershed and by ground-water inflow from the regional aquifer (Vionnet and Maddock, 1992).

Surface flow permanence and ground-water depth vary among sites due to geologic differences in depth to bedrock, proximity to tributaries, and proximity to sites of ground-water pumpage for agricultural, industrial, and/or municipal use (Heindl, 1952a,b; Goode and Maddock, 2000). Decades of ground-water pumping and surface diversions for municipal, industrial, and agricultural uses have contributed to lowered water tables and decreased base flows along the San Pedro River. In the Lower Basin, ground-water pumping for agricultural, mining, and municipal purposes has historically extracted approximately 6×10^7 m³/yr (Arizona Department of Water Resources, 1991). Within the Upper

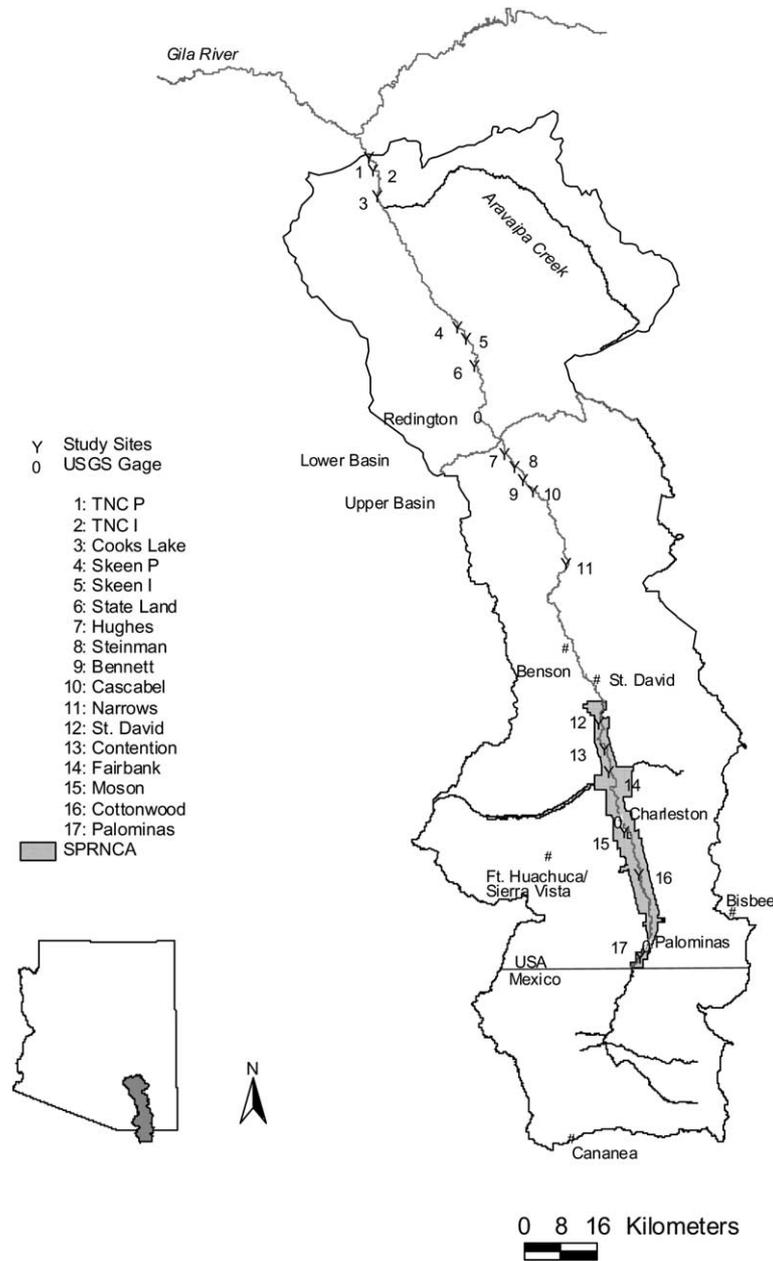


Fig. 1. Map of San Pedro River Basin showing study sites and locations of USGS stream gages. Direction of flow is from south to north.

Basin, Sierra Vista, Huachuca City, and the Ft. Huachuca military base are the largest population centers, obtaining the majority of their water supply from ground water. In recent decades these areas have pumped alluvial ground water at a rate exceeding its recharge from the regional aquifer. In apparent response to this pumping, base flows in the river and ground-water levels in the alluvial aquifer continue to decline (Goode and Maddock, 2000). In some reaches, a reverse pattern is apparent. For example, ground-water pumping at a copper mine near San Manuel (Lower Basin) has slowed as mining operations wind down.

Field data were collected during 2000–2002 from 17 sites along the San Pedro River from the International

border to the confluence with the Gila River (Fig. 1). Sites were preferentially placed in riparian preserves, to reduce confounding effects of land use factors, and were distributed so as to capture a range of hydrologic conditions along the San Pedro River (from strongly intermittent to perennial reaches), but otherwise were placed randomly. Most of the study sites were on riparian preserves, including the Bureau of Land Management’s San Pedro Riparian National Conservation Area (SPRNCA), which encompasses a 50 km section of the upper portion of the Upper Basin; Bureau of Land Management lands near Cascabel, in the upper part of the Lower Basin; the Bureau of Reclamation Cooks Lake riparian area, also in the Lower Basin; and The Nature Conservancy’s San

Pedro River Preserve which extends approximately 5 km in the lower portion of the Lower Basin, near the confluence with the Gila River. Four of the 17 sites were privately owned or were state of Arizona lands leased by citizens for livestock grazing. All sites have a history of livestock grazing, with cattle having been removed from the Upper Basin sites in 1988 with the creation of the SPRNCA and in 1988 through 1997 from most Lower Basin sites due to changes in land ownership.

2.2. Abundance, stand structure, and size structure

At each of the 17 sites, we established two transects perpendicular to the channel that spanned the width of the flood plain, extending to the base of the *Prosopis-Sporobolus* (mesquite-sacaton) terraces. Vegetation patch types along the two transects at each site were classified based on physiognomy and floristics, following rules developed for the National Vegetation Classification system (Grossman et al., 1998). Physiognomic classes included forest (canopy layer >60% cover), woodland (canopy 25–60%), shrubland (canopy <25% and mid-stratum >25%), grass- or forbland (canopy and mid-stratum <25% and groundcover >25%), and open (cover in all three strata <25%). Patch types were further divided based on composition and stem size class of the dominant woody species.

At one transect per site, 5 × 20 m study plots (long axis parallel to the river) were randomly placed in each discrete patch. The number of plots ranged from 7 to 28 among sites (total plots = 343), varying with the number of patches present, which itself varied with flood-plain width and site hydrology (Lite, 2003). There were multiple replicates of each patch type at most sites.

Within each study plot, data were collected on woody vegetation structure, for the stand as a whole and by woody species. Measurements included vegetation volume, canopy cover, canopy height, woody plant stem density, and woody plant basal area. Vegetation volume was measured using the vertical line intercept method, at three points per plot (Mills et al., 1991). A 9.5 m pole, marked in meters and decimeters, was extended vertically from the ground through the canopy and the number of decimeter hits per woody species was recorded within each meter interval. A hit is defined as any vegetation within a 10 cm radius of the pole, per vertical decimeter. Canopy heights above 9.5 m were estimated as either three or seven hits per interval, by species. These estimations were based on comparisons with lower intervals where hits could be directly measured. Total and per species vegetation volume values were calculated as the sum of all hits for each decimeter layer, divided by 10. The three values recorded for each plot were averaged. Maximum canopy height within plots was measured using either the vertical pole or a clinometer. Canopy cover was measured using a spherical densiometer at five points (plot corners and center) per plot. Stem density

was calculated by counting each live tree stem emerging from the ground in the study plots. Basal diameter of each stem was measured using a diameter tape or calipers.

Vegetation structure variables were then reduced to the site (flood-plain) level. Percent of the flood-plain transect line occupied by each patch type was calculated for both transects per site, and these two values were then averaged. The plot-level biomass structure values for a patch type were then weighted by the average width of the respective patch type at the site.

Importance values, which summarize the relative abundance of species, were used to determine community composition thresholds. Importance values were calculated using a modification of the Curtis and McIntosh (1951) formula: Importance value = (relative basal area + relative canopy cover + relative vegetation volume)/3. We calculated importance values only for the three dominant pioneer tree species: *P. fremontii*, *S. gooddingii*, and *T. ramosissima*. Because *S. gooddingii* and *P. fremontii* are ecologically similar, the importance value of these two species was summed. Thus, the reported importance value represents site values for the relative importance of *T. ramosissima* in relation to *P. fremontii* + *S. gooddingii*, and vice versa.

To characterize stem size class richness, *P. fremontii*, *S. gooddingii*, and *T. ramosissima* were arbitrarily broken into 5 cm diameter size categories; this size interval represents an approximate age range of 2–3 years for *P. fremontii* and *S. gooddingii* and of 7–20 years for *T. ramosissima* (Stromberg, 1998). Site values for total and per species numbers of size classes present were calculated by examining data from all plots sampled per site.

2.3. Site hydrology

River cross sections and flood-plain transects were surveyed using a transit and stadia rod (painted pole, calibrated in metric units), to determine plot elevation above and distance from channel thalweg (deepest point of channel). At each site, surface flow presence/absence, depth to ground water, and river stage (depth at thalweg) were monitored monthly (with synoptic sweeps across sites) during water years 2001 and 2002. (A water year, or hydrologic year, extends from October 1 to September 30 in the Northern Hemisphere, and corresponds to the annual cycle of hydrologic seasons; it commences with the maximum run-off season and terminates with the end of the maximum evapotranspiration season.) Surface flow was counted as present if there was water in the channel at the time of a monthly site visit. Surface flow permanence (a measure of the degree of intermittency) was calculated as the percentage of months during which surface flow was present over the two-year period, and is expressed as the percent of time that discharge exceeded zero.

Ground-water depth (specifically, depth to saturated soil) was measured monthly in monitoring wells. Some of the wells were in place at the beginning of the study (Stromberg et al., 1996; Stromberg, 1998). Additional wells were installed (hand-pounded) into the stream alluvium along the transect lines, such that there were two at each intermittent flow site (located approximately one-third and two-thirds of the distance from the channel to the terrace) and one at each perennial site (located halfway across the flood plain). The ground-water table under the flood plain was interpolated from the two well points at the intermittent flow transects, and from the river stage and well point at the perennial flow transects. In the absence of an extensive ground-water model, a linear ground-water table provides a reasonable approximation of depth to ground water across the flood plain. Depth to ground water across the flood plain was calculated as the difference between the land surface and ground-water elevations. Depth to ground water was characterized as the maximum depth to ground water at a site during the water year (spatially averaged across the flood plain). For statistical analyses, we used the means of the ground-water depth values measured in water years 2001 and 2002.

Water level fluctuation was calculated as the maximum difference between a January and a June water depth during the entire two-year study period, as measured in the well farthest from the stream edge at each site. There was a large flood in fall (October) of 2000 (Table 1) but there were no large winter floods during the study period and by January the aquifer has generally recovered from evapotranspiration losses. The main dry season for this region occurs in June, prior to the period of maximum evapotranspiration and the onset of the monsoon season. The January–June difference thus provides an estimate of annual ground-water fluctuation.

We assumed that the hydrology values measured over the two-year period represented average long-term conditions, given that stream flow rates were above average in one year (2001) and below average in the other (2002) (Table 1). Surface flows were high during 2001 due to recharge associated with a flood in October 2000. In contrast, mean annual flow for water year 2002 was below

average, reflecting the present drought conditions operating in Arizona. There was variation in the hydrologic variables between years; for example, the mean maximum depth to water in the wells closest to the edge of the flood plain was 3.8 ± 2.0 m in water year 2001 and 4.2 ± 1.8 m in 2002. However, there may be considerably more variation over the long-term; greater extremes of ground-water depths and flow intermittency undoubtedly occur during extended drought conditions.

2.4. Statistical analysis

Spearman rank order correlations and single and multiple regression were used to identify relationships between site-level vegetation metrics (dependent variables) and hydrologic metrics (independent variables). Multiple regression analysis indicated that some vegetation variables were related to three hydrologic variables (surface flow permanence, depth to ground water, and ground-water fluctuation) in concert. To integrate these three weekly correlated variables into a single metric, we calculated a variable we refer to as the hydrologic index. This was calculated as: Hydrologic index = $-(100 - \text{percent flow permanence}) * \text{maximum depth to ground water} * \text{water table fluctuation}$. A negative scale was used so that larger numbers (less negative) represented wetter conditions. The hydrologic index becomes increasingly negative as surface flow becomes more intermittent, ground-water depth declines, and/or as inter-annual ground-water fluctuation increases. For sites with perennial flow, flow permanence was entered into the formula as 99%, so as not to produce zero values for all such sites (and thereby discount the effects of the ground-water variables).

Regression plots (including 95% confidence interval curves) of importance value vs. the individual hydrologic variables and hydrologic index were used to determine hydrologic threshold values for three conditions of forest structure: (1) dominance of *T. ramosissima* (defined as values below the intersection of the lower 95% confidence interval curve for *T. ramosissima* and the upper 95% confidence interval curve for *P. fremontii* + *S. gooddingii*), (2) levels where *P. fremontii* and *S. gooddingii* are

Table 1

Mean annual hydrologic conditions along San Pedro River for water years 2001 and 2002 and the period of record, and instantaneous peak flow for October 2000 flood

	Water year 2001	Water year 2002	Period of record	October 2000
<i>Hydrologic variables measured at 17 San Pedro River sites</i>				
Flow permanence (%)	89	58	–	–
Depth to ground water (m)	3.8	4.2	–	–
<i>Flow rate values for USGS gages</i>				
Palominas (m ³ /s)	2.4	0.3	0.9	450
Charleston (m ³ /s)	2.5	0.3	1.6	494
Redington (m ³ /s)	1.5	0.1	1.2	139

Depth to ground water indicates mean annual maximum depth to ground water in well farthest from channel edge.

the dominant pioneer tree species (defined as the intersection of the upper 95% confidence interval curve for *T. ramosissima* and the lower 95% confidence interval curve for *P. fremontii* + *S. gooddingii*), and (3) levels at which *P. fremontii*–*S. gooddingii* and *T. ramosissima* are co-dominant (values in between the defined thresholds).

Statistical relationships were considered significant at the $p \leq 0.10$ level (as opposed to $p \leq 0.05$). We used this lower alpha level (and higher beta level) to reduce the risk of not detecting effects when they are present (Type II error), which is increasingly recognized as an important error type for biological conservation issues. Variables used in regression equations met assumptions for normality and constant variance. Statistical analyses were conducted using SAS version 8.2 (SAS Institute, 2001) and SigmaStat version 2.03 (SPSS, 1995).

3. Results

3.1. Hydrology

Two-year average flow permanence ranged among sites from 29% (i.e., stream water present in the channel about one-third of the time) to 100% (i.e., perennial flow). Sites ranged from 5.3 to 1.3 m in maximum depth to ground water (i.e., maximum value across the flood plain for each year, averaged), and from 1.5 to 0.05 m in

maximum January–June ground-water fluctuation. Hydrologic index ranged among sites from -0.0005 (wet) to -1.841 (dry). This driest site had flow permanence of 67%, maximum ground-water depth of 3.6 m, and inter-annual fluctuation of 1.52 m. The site with the second driest hydrologic index scored -1.45 , reflecting flow permanence of 33%, maximum ground-water depth of 3.7 m, and inter-annual fluctuation of 0.6 m.

3.2. Population and community structure

Most measures of *P. fremontii*, *S. gooddingii*, and *T. ramosissima* abundance varied among sites with flow permanence, some with ground-water depth, and a few with ground-water fluctuation (Table 2). *P. fremontii* and *S. gooddingii* canopy cover, vegetation volume, basal area, stem density, and stem size class richness increased with increasing flow permanence and/or decreasing depth to ground water. Three measures of *S. gooddingii* abundance increased with decreasing ground-water fluctuation. *S. gooddingii* and *P. fremontii* had greatest abundance where depth to ground water was <3.5 m; abundance of *S. gooddingii* declined sharply as ground-water fluctuation exceeded 0.5 m and *P. fremontii* declining as ground-water fluctuation exceeded about 0.8 m (Table 3). In contrast, *T. ramosissima* increased in abundance under drier conditions. Surface flow permanence and ground-water variables collectively explained

Table 2
Spearman rank order correlation coefficients between population level traits of three riparian tree/shrub species and San Pedro River hydrology

	Flow permanence	Depth to ground water	Ground-water fluctuation	Hydrologic index
<i>Populus fremontii</i>				
Canopy cover	0.64**	–	–	0.43*
Vegetation volume	0.46**	–0.51**	–	–
Lower canopy vegetation volume	0.45*	–	–	–
Upper canopy vegetation volume	0.54**	–0.46*	–	0.42*
Basal area	0.73**	–0.43*	–	0.55**
Stem density	0.51**	–0.44*	–	0.42*
Stem size class richness	0.70**	–0.47*	–	0.63**
<i>Salix gooddingii</i>				
Canopy cover	0.66**	–0.62**	0.40*	0.70**
Vegetation volume	0.54**	–0.54**	–	0.54**
Lower canopy vegetation volume	0.47*	–0.56**	–	0.48**
Upper canopy vegetation volume	0.47*	–	–	0.43*
Basal area	0.61**	–	0.43*	0.67**
Stem density	0.53**	–0.46*	–	0.59**
Stem size class richness	0.58**	–	0.42*	0.60**
<i>Tamarix ramosissima</i>				
Canopy cover	–0.54**	0.44*	–	–0.46*
Vegetation volume	–0.54**	–	–	–0.42*
Lower canopy vegetation volume	–0.57**	–	–	–0.43*
Upper canopy vegetation volume	–	–	–	–
Basal area	–0.45*	–	–	–
Stem density	–0.65**	–	–	–0.45*
Stem size class richness	–	–	–	–

Coefficients are shown only if significant ($n = 17$).

* $p < 0.10$.

** $p < 0.05$.

Table 3

Mean values for *P. fremontii*, *S. gooddingii*, and *T. ramosissima* abundance within San Pedro River sites classified by hydrologic variables

	<i>P. fremontii</i> basal area (m ² /ha)	<i>S. gooddingii</i> basal area (m ² /ha)	<i>T. ramosissima</i> basal area (m ² /ha)
<i>Surface flow permanence classes</i>			
100% (<i>n</i> = 5)	14.32	2.36	3.11
76–99% (<i>n</i> = 4)	13.60	2.78	2.87
50–75% (<i>n</i> = 5)	6.73	0.28	8.84
25–49% (<i>n</i> = 3)	1.55	0.43	9.76
<i>Ground-water depth classes</i>			
<2.5 m (<i>n</i> = 7)	10.46	2.31	3.75
2.5–3.5 m (<i>n</i> = 5)	13.89	1.48	6.07
3.5–4.5 m (<i>n</i> = 4)	4.34	0.40	8.78
>4.5 m (<i>n</i> = 1)	0.00	0.75	22.75
<i>Ground-water fluctuation classes</i>			
<0.5 m (<i>n</i> = 12)	11.25	2.06	4.92
0.5–0.8 m (<i>n</i> = 3)	8.09	0.22	6.43
>0.8 m (<i>n</i> = 2)	2.50	0.17	16.58

variance in several abundance measures including basal area (Table 4).

There were significant changes in community biomass structure as depth to ground water increased and surface flows became more intermittent, reflecting species composition shifts from *P. fremontii*–*S. gooddingii* to *T. ramosissima*. Because *T. ramosissima* generally has a shorter canopy than *P. fremontii* and *S. gooddingii*, there were declines in vegetation volume above 8 m, the number of 1-m layer strata that contained vegetation, and maximum canopy height, as sites became drier (Table 5)

and as *T. ramosissima* became dominant (Table 6). Physiognomy patterns mirror these vegetation volume and height patterns, with an increase in shrublands and decrease in woodlands at the drier sites (Table 5). The total richness of woody stem size classes also declined, reflecting the smaller number of size classes of *P. fremontii* and *S. gooddingii* present at the drier sites.

Total canopy cover, vegetation volume, basal area, and stem density did not vary as a function of site hydrology. The method we used to measure canopy cover detected vegetation above 1 m, where *T. ramosiss-*

Table 4

Results of multiple regression analysis relating the importance value of *T. ramosissima* (relative to *P. fremontii* + *S. gooddingii*), and the abundance (basal area) of *P. fremontii*, *S. gooddingii*, and *T. ramosissima*, to San Pedro River hydrologic variables

	Surface flow permanence	Depth to ground water	Ground-water fluctuation	Model <i>r</i> ²
<i>T. ramosissima</i> importance value	0.003	0.08	0.03	0.75
<i>P. fremontii</i> basal area	0.002	–	0.14	0.58
<i>S. gooddingii</i> basal area	0.04	–	–	0.24
<i>T. ramosissima</i> basal area	0.06	–	0.14	0.37

Values shown are the *p* value (level of significance in the model) for each independent variable and the model *r*² value (*n* = 17).

Table 5

Spearman rank order correlation coefficients between San Pedro River community structural traits and hydrology

	Flow permanence	Depth to ground water	Ground-water fluctuation	Hydrologic index
Canopy cover	–	–	–	–
Basal area	–	–	–	–
Stem density	–	–	–	–
Vegetation volume	–	–	–	–
Upper canopy vegetation volume	0.54**	–	–	0.40*
Stem size class richness	0.71**	–	–	0.55**
No. of 1-m vertical intervals with vegetation	0.64**	–0.46*	–	0.45*
Maximum vegetation height	0.65**	–	–	0.45*
Shrubland cover (%)	–0.41*	–	–	–0.48**
Woodland cover (%)	0.45*	–0.52**	0.63**	0.60**

Coefficients are shown only if significant (*n* = 17).

* *p* < 0.10.

** *p* < 0.05.

Table 6

Ranges, means, and standard deviations of population abundance and community traits within San Pedro River sites dominated by *P. fremontii*–*S. gooddingii*, those dominated by *T. ramosissima*, and those co-dominated by the three species (based on thresholds derived from Fig. 3)

	<i>P. fremontii</i> – <i>S. gooddingii</i> dominant (n = 12)	Mixed (n = 1)	<i>T. ramosissima</i> dominant (n = 4)
	Mean ± SD	Mean	Mean ± SD
<i>P. fremontii</i> + <i>S. gooddingii</i>			
Basal area (m ² /ha)	15 ± 7	5	2 ± 2
Canopy cover (%)	31 ± 20	11	3 ± 3
Vegetation volume (m ³ /ha)	7900 ± 5700	5600	700 ± 1300
<i>T. ramosissima</i>			
Basal area (m ² /ha)	3 ± 3	5	14 ± 9
Canopy cover (%)	8 ± 6	14	23 ± 7
Vegetation volume (m ³ /ha)	1800 ± 1600	6300	4100 ± 1600
Community structure			
Upper canopy vegetation volume (m ³ /ha)	6600 ± 4600	3100	900 ± 600
No. of 5 cm size classes	9 ± 2	7	5 ± 2
Maximum vegetation height (m)	20 ± 5	13	11 ± 4
Shrubland cover (%)	22 ± 12	8	48 ± 4
Woodland cover (%)	14 ± 7	24	2 ± 4

ima, *P. fremontii*, and *S. gooddingii* can all be abundant. Total stem density and basal area were independent of site hydrology because individual species patterns counter balanced each other: Whereas *T. ramosissima* basal area and stem densities were higher at the dry sites, *P. fremontii* and *S. gooddingii* basal area and stem densities increased at the wet sites. An additional species contributing substantially to stand stem density is *Baccharis salicifolia* (seep willow). This shrub often occurs along channel margins and in the understory of *P. fremontii*–*S. gooddingii* forests, and is slightly more abundant at wetter sites (Lite, 2003).

3.3. Community composition thresholds and threshold model

The relationship between importance value and the three hydrologic values was highly significant (Table 4).

Of the three independent variables in the multiple regression model, surface flow permanence explained most of the variance in the *Tamarix* vs. *Populus*–*Salix* importance value, followed respectively by ground-water fluctuation and ground-water depth. Based on examination of 95% confidence intervals (Fig. 2), *P. fremontii*–*S. gooddingii* were the dominant pioneer species at sites where flow permanence was greater than 76%, January–June ground-water fluctuation was less than 0.5 m, and ground-water depth shallower than 2.6 m (Table 7). At sites where flow permanence was <42%, *T. ramosissima* was dominant. *P. fremontii*–*S. gooddingii* and *T. ramosissima* co-dominated at intermediate flow permanence values. Using the 95% confidence interval approach, ground-water depth and fluctuation threshold values for dominance by *T. ramosissima* could not be determined (Table 7). The same was true for the 90%

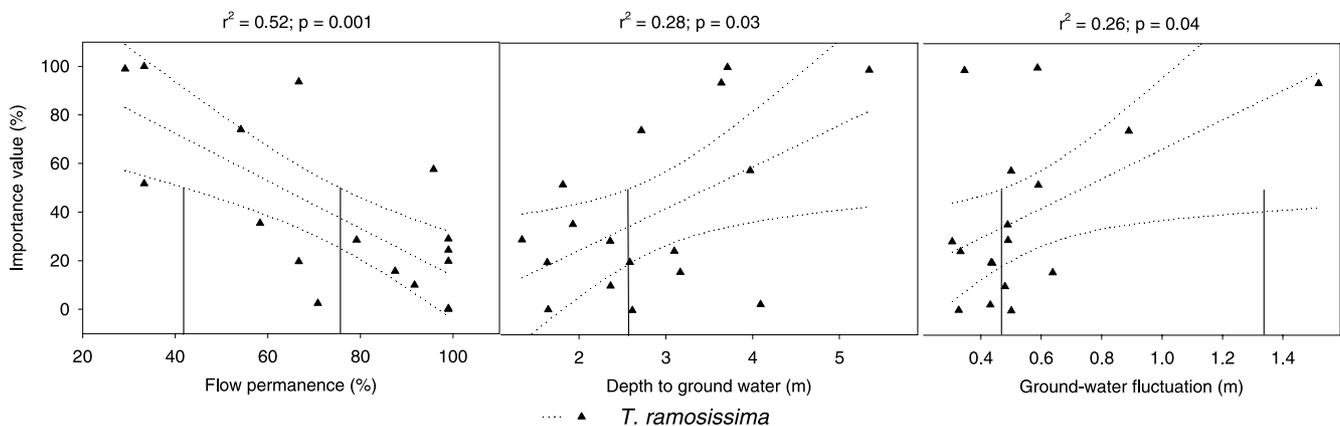


Fig. 2. Regression relation (with 95% confidence intervals) between *T. ramosissima* importance values and three San Pedro River hydrology variables. For clarity, the *P. fremontii* + *S. gooddingii* importance value is not shown. Upper and lower thresholds are evident for flow permanence, based on crossing points of the *T. ramosissima* and *P. fremontii* + *S. gooddingii* importance value confidence intervals; only upper thresholds are evident for depth to ground water and ground-water fluctuation.

Table 7

Hydrologic threshold ranges for the dominance of *P. fremontii*–*S. gooddingii* and *T. ramosissima* along the San Pedro River

	Flow permanence (%)	Depth to ground water (m)	Ground-water fluctuation (m/yr)	Hydrologic index
<i>P. fremontii</i> – <i>S. gooddingii</i>	>76	<2.6	<0.46	>–0.53
Co-dominant	42 to 76	>2.6	>0.46	–0.92 to –0.53
<i>T. ramosissima</i>	<42	–	–	<–0.92

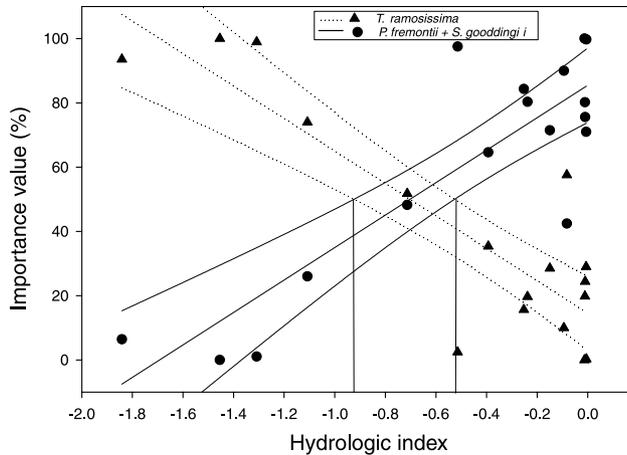


Fig. 3. Regression lines (with 95% confidence intervals) showing hydrologic thresholds for the maintenance of *P. fremontii*–*S. gooddingii* stands along the San Pedro River. Higher hydrologic index values indicate wetter conditions.

confidence intervals (data not shown). A larger sample of very dry sites is needed to conclusively pinpoint these lower thresholds.

The thresholds just discussed are based on analysis of individual hydrologic variable-importance value relationships. However, the hydrologic variables collectively influence species composition. The relationship between importance value and hydrologic index (i.e., the integrated hydrology variable) was highly significant ($r^2 = 0.75$; $p < 0.001$; Fig. 3). With respect to the integrated hydrologic index, *P. fremontii*–*S. gooddingii* were dominant at values greater than -0.5 , while *T. ramosissima* dominated where values were less than -0.9 (Fig. 3, Table 7). Given that the hydrologic index is a product of three variables, a value of -0.9 could be produced by several permutations, such as by a flow duration of 60%, ground-water depth of 3 m, and fluctuation of 0.7 m, or by a flow duration of 70%, ground-water depth of 3.5 m, and fluctuation of 0.9 m.

4. Discussion

4.1. Causes of shifts in species dominance

We hypothesized that changes in ground water-depth and fluctuation would be the prime drivers of *P. fremontii*–*S. gooddingii* abundance and of composition

shifts from *Populus*–*Salix* to *T. ramosissima* within the riparian flood plain of the San Pedro River. Although both of these hydrologic variables were related to species abundance and to the compositional shift, the variable that explained the most variance was, surprisingly, surface flow permanence. Relationships of species abundances with flow permanence were often stronger than with the ground-water variables, suggesting that, directly or indirectly, surface flow permanence is an important indicator of San Pedro River forest composition and structure. Surface water can provide a water source for young trees that line the low-flow channel (Smith et al., 1991), and surface water can raise local humidity levels and provide an essential buffer to high evaporation rates along arid region rivers. Low humidity and high leaf-to-air vapor pressure deficits at intermittent sites may contribute to reduced photosynthetic rates of some species despite shallow ground-water tables (Horton et al., 2001a). However, we suspect that surface flow permanence in the threshold model and other relationships likely serves as a surrogate for the degree of long-term ground-water fluctuation under the flood plain, rather than as a direct influence on vegetation. Sites with perennial flow tend to be situated in gaining reaches, where inflowing ground water would sustain stable, shallow ground-water levels across the flood plain even during times of extended drought. At the highly intermittent sites, which typically are in losing reaches, ground-water depths and fluctuations likely have periodically exceeded the levels observed in this two-year study, and exceeded survivorship tolerance ranges for *P. fremontii* and *S. gooddingii*.

Although flow permanence was a key driver, ground-water depth also influenced species abundance and community composition. The ground-water depth thresholds at which *P. fremontii*–*S. gooddingii* stands maintain dominance over *T. ramosissima* (2.6 m) along the San Pedro River, and the values below which *P. fremontii* and *S. gooddingii* had low abundance (ca. 3.5 m), are consistent with values reported for the survival of mature *Populus* and *Salix* spp. along other rivers in the Sonoran desert biomes (Table 8). At the Hassayampa River, for example, *S. gooddingii* and *P. fremontii* trees both underwent physiological stress, observed as canopy dieback and reduced photosynthetic rates, as depth to ground water exceeded 3 m, with *S. gooddingii* undergoing the

Table 8
Ground-water depth and decline rate thresholds for survival of *Populus* and *Salix* species

Species	Ground-water factor	Value	Location	Reference
Sapling survival				
<i>P. fremontii</i> <i>S. gooddingii</i>	Maximum depth	2.91 m	Bill William River, AZ where water table had regular inter-annual fluctuations	Shafroth et al. (2000)
<i>P. fremontii</i> <i>S. gooddingii</i>	Maximum depth	0.82 and 3.14 m	Bill Williams River, AZ sites where water tables were relatively shallow and stable	Shafroth et al. (2000)
<i>P. fremontii</i>	Maximum depth	2.93 m	Bill Williams River, AZ	Shafroth et al. (1998) ^a
<i>S. gooddingii</i>	Maximum depth	2.02 m	Bill Williams River, AZ	Shafroth et al. (1998) ^a
<i>P. fremontii</i>	Maximum depth	2 m	San Pedro River, AZ	Stromberg et al. (1996)
<i>S. gooddingii</i>				
<i>P. fremontii</i>	Maximum depth	1 m	Hassayampa River, AZ	Stromberg et al. (1991)
Adult survival				
<i>P. fremontii</i> <i>S. gooddingii</i>	Maximum depth	2.5–3 m	Hassayampa River, AZ	Horton et al. (2001a) ^a and Horton et al. (2001b) ^a
<i>P. fremontii</i>	Maximum depth	2.6 m	Hassayampa River, AZ	Stromberg et al. (1991)
<i>P. fremontii</i>	Maximum depth	5.1 m	San Pedro River, AZ	Stromberg et al. (1996)
<i>S. gooddingii</i>	Maximum depth	3.2 m	San Pedro River, AZ	Stromberg et al. (1996)
<i>P. deltoides</i>	Decline rate	1 m/yr	Coal Creek, CO	Scott et al. (1999) ^a
<i>P. fremontii</i>	Decline rate	1.1 or 2.28 m/yr	Bill Williams River, AZ	Shafroth et al. (2000)
<i>S. gooddingii</i>				

Values are maximum depths or rates at which species occurred.

^a Studies designed to detect threshold values, other values are for observed ranges of occurrence.

greatest ground-water related mortality (Horton et al., 2001b). On the Bill Williams River, where river regulation has produced stable seasonal ground-water levels, both species were in good physiological condition at sites where depth to ground water was less than 4 m (Horton et al., 2001a).

The extent of inter-annual ground-water fluctuation also was significantly related to abundance of the riparian trees and to compositional shifts from *Populus*–*Salix* to *Tamarix*. The *Populus* and *Salix* spp. roots that are primarily responsible for water uptake occur in the zone of moisture extending above the zone of saturation called the capillary fringe (Mahoney and Rood, 1998). Because fine roots are concentrated in the capillary fringe, these species are sensitive to fluctuation in water table depth, particularly in the coarse sediments that typify low-elevation southwestern river flood plains. Ground-water level decline during the hot summer dry season can strand roots above the water level and reduce tree productivity and, in some cases, cause death (Mahoney and Rood, 1992). Seasonal declines of 1 m have caused mortality of saplings of cottonwood and willow (Shafroth et al., 2000). Mature cottonwood trees have been killed by abrupt, permanent drops in water table of 1 m, with lesser declines (0.5 m) reducing stem growth (Scott et al., 1999, 2000). Because *T. ramosissima* can more effectively extract water from unsaturated soil, has deeper roots, and has higher water use efficiency, it can tolerate a wider range of ground-water fluctuations and depths than *P. fremontii* and *S. gooddingii* (Busch and Smith, 1995; Busch et al., 1992; Shafroth et al., 2000).

The water table decline values reported in the literature are similar to or greater than values we found to be favorable for *P. fremontii* (<ca. 0.8 m) and *S. gooddingii* (ca. 0.5 m) abundance, and for maintaining dominance of these species over *T. ramosissima* (0.5 m). These values can vary with several factors, including sediment texture. The vertical extent of the capillary fringe depends on soil texture and can range from 1.5 cm in fine gravel to 100 cm in very fine sand and 750 cm in fine silt (Fetter, 1994). The history of ground-water depths and fluctuations experienced by a plant population also can be important. A dramatic decline in ground-water depth relative to the level at which roots developed may strand roots above the water table, rendering thresholds sensitive to antecedent conditions. Shafroth et al. (2000) found that *P. fremontii* and *S. gooddingii* saplings survived at sites with greater depth to ground water when there were regular (but small) inter-annual fluctuations, compared to sites where the water table was relatively shallow and stable.

Hydrologic requirements for *P. fremontii*–*S. gooddingii* population maintenance vary across life stages, from seedlings to adults. Seedling establishment requirements are specific and narrow, and the hydrologic threshold values reported in this study predominantly reflect conditions required for adult survivorship. However, the stand structure values reported here (e.g., stem density and size class diversity) reflect recruitment and mortality processes ranging from seedling establishment to adult survivorship. *P. fremontii* and *S. gooddingii* size class diversity and stem density were low at dry sites, perhaps

due to reduced germination rate and/or increased mortality of sensitive young age classes. Water stress effects are often most pronounced in the juveniles of a species (Smith et al., 1991). At dry sites, ground-water depths may recede too rapidly and too deeply following floods to sustain seedlings, resulting in recruitment success only in very wet years. Ground-water declines exceeding 1 to 4 cm per day can result in *Populus* spp. seedling death (Mahoney and Rood, 1992; Shafroth et al., 1998; Amlin and Rood, 2002), as can end-of-season ground-water depths that exceed 1 to 1.3 m under recruitment bars (Stromberg et al., 1991; Shafroth et al., 1998). Low size class diversity at the dry sites may also occur because mortality thresholds for older plants are exceeded more frequently. Very large *P. fremontii* trees (basal diameter >100 cm) were present only at wetter sites. Presence of old-growth trees indicates that hydrologic conditions have consistently been sufficiently wet to sustain long-term survivorship, although absence of old trees may reflect vagaries of site history such as land clearing or extreme flooding.

4.2. Use of the threshold model

Thresholds can be used as management guidelines in various ways (Richter and Richter, 2000; Eiswerth and Haney, 2001). One type of threshold is a critical threshold, defined as small changes in physical conditions that produce abrupt and dramatic ecological responses (With and Crist, 1995). This type of threshold, observed in disciplines ranging from landscape ecology (Boutin and Herbert, 2002) to geomorphology (Church, 2002), can be irreversible in the absence of a dramatic change to the system. The hydrologic thresholds identified for the maintenance of dense *P. fremontii*–*S. gooddingii* stands along the San Pedro River are probably not critical thresholds. If shallow ground-water levels were restored, the current pattern of frequent flooding should allow for the gradual (one to two decades) replacement of *T. ramosissima* stands by *P. fremontii*–*S. gooddingii* forests.

The hydrologic thresholds for *P. fremontii*–*S. gooddingii* stand maintenance identified here resemble Rogers and Biggs (1999) “thresholds of probable concern”, which they define as warnings for potential “unacceptable environmental change” and “scientifically described endpoints for ecosystem management”. The San Pedro River hydrologic thresholds can be used to help define management goals and alert managers to the potential for species shifts from *P. fremontii*–*S. gooddingii* stands to mixed stands of *P. fremontii*–*S. gooddingii*–*T. ramosissima* as hydrologic values drop below the top threshold, and to *T. ramosissima* stands as values drop below the bottom threshold. As hydrologic conditions change along the San Pedro, there is great interest by local land managers, including the Bureau of Land Management and The Nature Conservancy, to conserve and restore

the *P. fremontii*–*S. gooddingii* forest community and to track ecological changes subsequent to decreases (and increases) in ground-water extraction. For example, The Nature Conservancy recently purchased approximately 1000 ha and associated water rights within the Lower Basin with the intention of dramatically reducing ground-water pumping and allowing *P. fremontii* and *S. gooddingii* to reestablish. It is expected that once ground-water and surface flow levels are increased, the *P. fremontii*–*S. gooddingii* stands will gradually replace the *T. ramosissima* stands (Stromberg, 1998).

These thresholds are not actual predictive hydrologic values for conditions at which *P. fremontii*–*S. gooddingii* forests yield to *T. ramosissima* stands because we used a space-for-time substitution in which dry sites are inferred representative of future dewatered conditions. This assumes that plant communities are adjusted to current conditions, although this may not be the case if there are lag-times associated with an increase or decrease in water availability, or with other factors such as cattle grazing. The relative abundance of *T. ramosissima* along the San Pedro River may be high due to past grazing influences, given that selective browsing on *P. fremontii* and *S. gooddingii* can favor *T. ramosissima* survival (Stromberg, 1997). Stream flow rates and ground-water depths along the river have varied over time in association with severe drought periods (such as occurred in the 1950s) and with changes in local land- and water-use practices.

Monitoring of vegetation and hydrology along the San Pedro River, in reaches undergoing changes in water availability, can serve to test the accuracy of the threshold model. All three hydrologic components of the model (stream flow permanence and ground-water depth and fluctuation) should be monitored, as should the riparian community directly. As well, the threshold model also should be tested (validated) using sites along other southwestern rivers such as the Hassayampa and Bill Williams Rivers, and the Rio Grande.

4.3. Threshold model applicability to invasive species management

The hydrologic thresholds presented here emphasize that restoring hydrologic processes may allow the Sonoran riparian species to regain dominance over the introduced *Tamarix* without further human intervention, and that *T. ramosissima* abundance can be reduced by restoring hydrologic conditions favorable to *Populus* spp. and *Salix* spp. Dewatering-induced species replacements are occurring throughout the southwest (Busch and Smith, 1995; Sala et al., 1996; Horton et al., 2001b) and restoration projects increasingly are being implemented to restore *P. fremontii* and *S. gooddingii* to areas dominated by *T. ramosissima* (Taylor and McDaniel, 1998; Springer et al., 2002; Smith et al., 2002). Many projects

involve only the removal of *T. ramosissima*, or removal followed by planting of *P. fremontii* and/or *S. gooddingii*. Projects that do not focus on the underlying causes of species replacement are often unsustainable and slated for long-term failure. A more ecologically viable approach to river restoration and *Tamarix* spp. management involves restoring the environmental conditions under which desired species, such as *P. fremontii* and *S. gooddingii*, are more competitive (Poff et al., 1997; Stromberg, 1998; Stromberg and Chew, 2002).

The *Populus–Salix* vs. *Tamarix* threshold model is based on a subset of the environmental factors that influence riparian plant species composition (i.e., on low-flow components of the hydrologic regime) and is applicable only if other environmental conditions required for establishment of *Populus–Salix* are present, and those favorable to *T. ramosissima* are absent. Several management actions and environmental conditions may modify or override these observed hydrologic thresholds. For example, with high livestock grazing pressure, *T. ramosissima* could dominate even at sites with perennial stream flows and shallow ground-water tables. There are many changes that can arise due to river damming that influence species composition. Along dammed rivers that have perennial flow and shallow ground-water tables but lack the flood pulses of appropriate timing and rate of change necessary for *P. fremontii* and *S. gooddingii* establishment, *T. ramosissima* may dominate (Shafroth et al., 2002; Cooper et al., 2003). Altered timing of summer flow releases from dams, or of water recession levels on reservoir edges, can favor establishment of the more reproductively opportunistic *T. ramosissima* (Tallent-Halsell and Walker, 2002) as may below-dam reduction in the frequency of the scouring floods that cause seedling mortality (Levine and Stromberg, 2001).

Another factor that can vary below dams is the frequency of the depositional overbank flood flows that add moisture and nutrients to the soil column. Depending on spatial and temporal patterns of water availability, *P. fremontii*, *S. gooddingii*, and *T. ramosissima* may use varying combinations of ground water, soil water (water in the unsaturated zone) and surface flows (Busch et al., 1992; Smith et al., 1998). The ability of riparian plants to utilize this shallow soil water depends on their ability to access water from unsaturated soils; as a facultative phreatophyte, *T. ramosissima* may be better suited than *P. fremontii* and *S. gooddingii* to do so (Busch et al., 1992). Use of water from unsaturated soils by *T. ramosissima* increases at sites with frequent inundation (Cleverly et al., 2002). Although the frequency of overbank flooding can decline on flow-regulated rivers, the stability of the ground-water table can increase (Shafroth et al., 2002). Effects of dam operation on water source (and nutrient) availability and use by *Populus*, *Salix* and *Tamarix* warrant further investigation.

Salinity levels also influence riparian species composition. Variable precipitation and high evaporation rates often lead to saline surface- and ground water in hot, arid regions. This process can be exacerbated by river impoundment, which decreases the frequency of flushing flows, and by runoff from irrigated agricultural land. At low salinity levels, *T. ramosissima*, *P. fremontii*, and *S. gooddingii* had similar water use rates, however as salinity increased, *T. ramosissima* extracted more water and had higher growth rates than did *P. fremontii* and *S. gooddingii* (Busch and Smith, 1995; Vandersande et al., 2001). The comparatively poor tolerance of *P. fremontii* and *S. gooddingii* to high salinity may shift community maintenance thresholds towards wetter conditions (such as shallower and more stable ground-water depths) under more saline conditions.

The *P. fremontii–S. gooddingii* forest ecosystem type occurs over an elevation range from near sea level (e.g., lower Bill Williams and Colorado Rivers) to approximately 1600 m (e.g., upper San Pedro River) (Minckley and Brown, 1994). Although *T. ramosissima* occurs at elevations up to 3350 m, it may be less competitive than *Populus* and *Salix* at higher elevations that are cooler and more moist because plants may be under less transpirational stress (Lesica and Miles, 2001). *P. fremontii* and *S. gooddingii* may tolerate greater ground-water fluctuations in cold and wet climates and thus deeper average ground-water depths, and threshold values might shift accordingly.

4.4. Functional significance of changes in community structure

The structural changes of the San Pedro River forest we observed across spatial gradients of water availability can affect ecologic functions such as animal habitat provision and geomorphic processes. When structural characteristics are similar, *T. ramosissima* forests can have similar ecological functions to *P. fremontii* forests (Brown and Trosset, 1989; Ellingson and Andersen, 2002). *T. ramosissima* stands may supply critical habitat where broad-leafed deciduous species are absent or reduced (Brown and Trosset, 1989) and can contribute to abundance of particular animal species when part of a complex flood-plain mosaic (Taylor, 2003). However, shifts in community composition from *P. fremontii–S. gooddingii* to *T. ramosissima* can affect animal species richness, diversity, and abundance, due in part to structural differences of the stands and in part to abiotic effects such as site drying that are driving the vegetation change (Hunter et al., 1988; Ellis et al., 1997; Bailey et al., 2001). Shifts in vegetation volume and vertical and horizontal canopy structure could have implications for avian species, such as a decrease in richness and breeding bird density as total vegetation volume decreases (Mills et al., 1991; Fleishman et al., 2003). With respect to

geomorphic changes, further investigation on the San Pedro River, as well as other arid-region rivers, is needed to assess whether vegetation changes produce effects on sedimentation, channel migration, overbank flooding, or channel down cutting as sites become drier.

Although *T. ramosissima* typically has more stems per plant than do *P. fremontii* and *S. gooddingii*, we did not find total site stem density to increase at the drier sites, partly due to declines in abundance of another high stem-density shrub, *B. salicifolia*. Increases in stem density can be ecologically significant because of resulting increases in channel and flood-plain roughness which can cause geomorphic adjustments such as bank stabilization, increased overbank flooding, channel incision, and decreased channel migration (Graf, 1978).

Acknowledgments

This project was funded by the US Environmental Protection Agency's Water and Watershed Research Program, the National Science Foundation's Center for Sustainability of Semi-Arid Hydrology and Riparian Areas, and the Southwest Center for Environmental Research and Policy. We thank the land owners who allowed us to access their property: Arizona Nature Conservancy, Arizona State Lands Department, Barbara Clark, Carole and Mack Skeen, US Bureau of Land Management, and US Bureau of Reclamation. Ken Bagstad assisted in ground-water well installation and hydrologic data collection. Mark Dixon assisted with some of the statistical analysis. We are also grateful for the hard work of many people who assisted us in the field.

References

- Amlin, N.M., Rood, S.B., 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands* 22, 338–346.
- Arizona Department of Water Resources, 1991. Hydrographic Survey Report for the San Pedro River Watershed. Filed with the Court: November 20, 1991.
- Bailey, J.K., Schweitzer, J.A., Whitham, T.G., 2001. Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. *Wetlands* 21, 442–447.
- Boutin, S., Herbert, D., 2002. Landscape ecology and forest management: developing an effective partnership. *Ecological Applications* 12, 390–397.
- Brown, B.T., Trosset, M.W., 1989. Nesting-habitat relationships of riparian birds along the Colorado River in Grand Canyon, Arizona. *The Southwestern Naturalist* 34, 260–270.
- Busch, D.E., Smith, S.D., 1995. Mechanisms associated with the decline of woody species in riparian ecosystems of the Southwestern US. *Ecological Monographs* 65, 347–370.
- Busch, D.E., Ingraham, N.L., Smith, S.D., 1992. Water uptake in riparian phreatophytes of the Southwestern US: a stable isotope study. *Ecological Applications* 2, 450–459.
- Church, M., 2002. Geomorphic thresholds in riverine landscapes. *Freshwater Biology* 47, 541–557.
- Cleverly, J.R., Dahm, C.N., Thibault, J.R., Gilroy, D.J., Allred Coonrod, J.E., 2002. Seasonal estimates of actual evapotranspiration from *Tamarix ramosissima* stands using three-dimensional eddy covariance. *Journal of Arid Environments* 52, 181–197.
- Cleverly, J.R., Smith, S.D., Sala, A., Devitt, D.A., 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. *Oecologia* 111, 12–18.
- Cooper, D.J., Andersen, D.C., Chimner, R.A., 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. *Journal of Ecology* 91, 182–196.
- Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32, 476–498.
- Eiswerth, M.E., Haney, J.C., 2001. Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter. *Ecological Economics* 38, 259–274.
- Ellingson, A.R., Andersen, D.C., 2002. Spatial correlations of *Diceroprocta apache* and its host plants: evidence for a negative impact from *Tamarix* invasion. *Ecological Entomology* 27, 16–24.
- Ellis, L.M., Crawford, C.S., Molles Jr., M.C., 1997. Rodent communities in native and exotic riparian vegetation in the middle Rio Grande valley of central New Mexico. *The Southwestern Naturalist* 42, 13–19.
- Fetter, C.W., 1994. *Applied Hydrogeology*, third ed. Prentice-Hall Inc., Upper Saddle River, NJ, USA.
- Fleishman, E., McDonal, N., MacNally, R., Murphy, D.D., Walters, J., Floyd, T., 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. *Journal of Animal Ecology* 72, 484–490.
- Gaskin, J.F., Schaal, B.A., 2002. Hybrid *Tamarix* widespread in US invasion and undetected in native Asian range. *Proceedings of the National Academy of Sciences* 99, 11256–11259.
- Goode, T.C., Maddock III, T., 2000. Simulation of groundwater conditions in the Upper San Pedro Basin for the evaluation of alternative futures. University of Arizona, Department of Hydrology and Water Resources (HWR-00-030), Tucson, AZ, USA.
- Graf, W.L., 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. *Geological Society of America Bulletin* 89, 1491–1501.
- Grossman, D.H., Faber-Langendoen, D., Weakly, A.S., Anderson, M., Bourgeron, P., Crawford, R., Goodin, K., Landaal, S., Metzler, K., Patterson, K.D., Pyne, M., Reid, M., Sneddon, L., 1998. *International Classification of Ecological Communities: Terrestrial Vegetation of the United States The National Vegetation Classification System: development, status, and applications (vol. 1)*. The Nature Conservancy, Arlington, VA, USA.
- Heindl, L.A., 1952a. Upper San Pedro basin, Cochise county. In: Halpenny, L.C. (Ed.), *Ground Water in the Gila River Basin and Adjacent Areas, Arizona – A Summary*. US Geological Survey Open-file Report, Tucson, AZ, USA, pp. 69–86.
- Heindl, L.A., 1952b. Lower San Pedro basin, Cochise county. In: Halpenny, L.C. (Ed.), *Ground Water in the Gila River Basin and Adjacent Areas, Arizona – A Summary*. US Geological Survey Open-file Report, Tucson, AZ, USA, pp. 87–100.
- Horton, J.L., Kolb, T.E., Hart, S.C., 2001a. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications* 11, 1046–1059.
- Horton, J.L., Kolb, T.E., Hart, S.C., 2001b. Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell and Environment* 24, 293–304.
- Horton, J.S., 1964. Notes on the introduction of deciduous tamarisk. US Forest Service Research Note RM-16. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA.
- Hunter, W.C., Ohmart, R.D., Anderson, B.W., 1988. Use of exotic saltcedar (*Tamarix chinensis*) by birds in arid riparian systems. *The Condor* 90, 113–123.

- Leffler, A.J., England, L.E., Naito, J., 2000. Vulnerability of fremont cottonwood (*Populus fremontii* Wats.) individuals to xylem cavitation. *Western North American Naturalist* 60, 204–210.
- Lesica, P., Miles, S., 2001. Tamarisk growth at the northern margin of its naturalized range in Montana, USA. *Wetlands* 21, 240–246.
- Levine, C.M., Stromberg, J.C., 2001. Effects of flooding on native and exotic plant seedlings: implications for restoring south-western riparian forests by manipulating water and sediment flows. *Journal of Arid Environments* 49, 111–131.
- Lite, S.J., 2003. San Pedro River riparian vegetation across water availability and flood disturbance gradients. Ph.D. Dissertation, Department of Geography, Arizona State University, Tempe, AZ, USA.
- Mahoney, J.M., Rood, S.B., 1992. Response of a hybrid poplar to water table decline in different substrates. *Forest Ecology and Management* 54, 141–156.
- Mahoney, J.M., Rood, S.B., 1998. Streamflow requirements for cottonwood seedling recruitment – an integrative model. *Wetlands* 18, 634–645.
- Mills, G.C., Dunning Jr., J.B., Bates, J.M., 1991. The relationship between breeding bird density and foliage volume. *Wilson Bulletin* 103, 468–479.
- Minckley, W.L., Brown, D.E., 1994. Wetlands. In: Brown, D.E. (Ed.), *Biotic Communities of Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, UT, USA, pp. 223–301.
- NatureServe, 2003. NatureServe Explorer: An Online Encyclopedia of Life [web application]. Version 1.8. NatureServe, Arlington, VA, USA. Available from: <<http://www.natureserve.org/explorer>>.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime: a paradigm for river conservation and restoration. *Bioscience* 47, 769–784.
- Quimby Jr., P.C., DeLoach, C.J., Wineriter, S.A., Goolsby, J.A., Sobhian, R., Boyette, C.D., Abbas, H.K., 2003. Biological control of weeds: research by the United States Department of Agriculture – Agricultural Research Service: selected case studies. *Pest Management Science* 59, 671–680.
- Richter, B.D., Richter, H.E., 2000. Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. *Conservation Biology* 14, 1467–1478.
- Rogers, K., Biggs, H., 1999. Integrating indicators, endpoints and value systems in strategic management of the rivers of the Kruger National Park. *Freshwater Biology* 41, 439–451.
- Sala, A., Smith, S.D., Devitt, D.A., 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave desert floodplain. *Ecological Applications* 6, 888–898.
- SAS Institute, 2001. SAS/STAT User's Guide, Release 8.2. SAS Institute, Cary, NC, USA.
- Scott, M.L., Shafroth, P.B., Auble, G.T., 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management* 23, 347–358.
- Scott, M.L., Lines, G.C., Auble, G.T., 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. *Journal of Arid Environments* 44, 399–414.
- Sexton, J.P., McKay, J.K., Sala, A., 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecological Applications* 12, 1652–1660.
- Shafroth, P.B., Auble, G.T., Stromberg, J.C., Patten, D.T., 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* 18, 577–590.
- Shafroth, P.B., Stromberg, J.C., Patten, D.T., 2000. Woody riparian vegetation response to different alluvial water table regimes. *Western North American Naturalist* 60, 66–76.
- Shafroth, P.B., Stromberg, J.C., Patten, D.T., 2002. Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications* 12, 107–123.
- Sher, A.A., Marshall, D.L., 2003. Seedling competition between native *Populus deltoides* (Salicaceae) and exotic *Tamarix ramosissima* (Tamaricaceae) across water regimes and substrate types. *American Journal of Botany* 90, 413–422.
- Sher, A.A., Marshall, D.L., Gilbert, S.A., 2000. Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. *Conservation Biology* 14, 1744–1754.
- Sher, A.A., Marshall, D.L., Taylor, J.P., 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. *Ecological Applications* 12, 722–760.
- Smith, L.M., Sprenger, M.D., Taylor, J.P., 2002. Effects of discing saltcedar seedlings during riparian restoration efforts. *The Southwestern Naturalist* 47, 598–642.
- Smith, S.D., Wellington, A.B., Nachlinger, J.L., Fox, C.A., 1991. Functional responses of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. *Ecological Applications* 1, 89–97.
- Smith, S.D., Devitt, D.A., Sala, A., Cleverly, J.R., Busch, D.E., 1998. Water relations of riparian plants from warm desert regions. *Wetlands* 18, 687–695.
- Snyder, K.A., Williams, D.G., 2000. Water sources used by riparian trees varies among stream types on the San Pedro River. *Journal of Agricultural and Forest Meteorology* 105, 227–240.
- Sprenger, M.D., Smith, L.M., Taylor, J.P., 2002. Restoration of riparian habitat using experimental flooding. *Wetlands* 22, 49–57.
- SPSS, 1995. SigmaStat Version 2.03. SPSS Inc., Chicago, IL, USA.
- Stromberg, J.C., 1997. Growth and survivorship of Fremont cottonwood, Goodding willow, and salt cedar seedlings after large floods in central Arizona. *Great Basin Naturalist* 57, 198–208.
- Stromberg, J.C., 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40, 133–155.
- Stromberg, J.C., Chew, M.K., 2002. Foreign visitors in riparian corridors of the American Southwest: is xenophobia justified? In: Tellman, B. (Ed.), *Invasive Exotic Species in the Sonoran Region*. The University of Arizona Press and The Arizona-Sonora Desert Museum, Tucson, AZ, USA, pp. 195–219.
- Stromberg, J.C., Patten, D.T., Richter, B.D., 1991. Flood flows and dynamics of Sonoran riparian forests. *Rivers* 2, 221–235.
- Stromberg, J.C., Tiller, R., Richter, B., 1996. Effects of ground water decline on riparian vegetation of semi-arid regions: The San Pedro River, AZ. *Ecological Applications* 6, 113–131.
- Tallent-Halsell, N.G., Walker, L.R., 2002. Responses of *Salix gooddingii* and *Tamarix ramosissima* to flooding. *Wetlands* 22, 776–785.
- Taylor, J.P., McDaniel, K.C., 1998. Restoration of saltcedar (*Tamarix* sp.)-infested floodplains on the Bosque del Apache National Wildlife Refuge. *Weed Technology* 12, 345–352.
- Taylor, R.V., 2003. Factors influencing expansion of the breeding distribution of Bewick's wren into riparian forests of the Rio Grande in central New Mexico. *Southwestern Naturalist* 48, 373–382.
- Tuan, Y., 1962. Structure, climate, and basin land forms in Arizona and New Mexico. *Annals of the Association of American Geographers* 52, 51–68.
- Vandersande, M.W., Glenn, E.P., Walworth, J.L., 2001. Tolerance of five riparian plants from the lower Colorado River to salinity, drought and inundation. *Journal of Arid Environments* 49, 147–159.
- Vionnet, L.B., Maddock, T., 1992. Modeling of ground-water flow and surface water/ground-water interactions in the San Pedro River basin. Part I. Mexican border to Fairbank, Arizona. University of Arizona, Department of Hydrology and Water Resources Report 92-010, Tucson, AZ, USA.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76, 2446–2459.
- Zavaleta, E., 2000. Valuing ecosystem services lost to *Tamarix* invasion in the United States. In: Mooney, H.A., Hobbs, R.J. (Eds.), *Invasive Species in a Changing World*. Island Press, Washington, DC, USA, pp. 261–300.